On the Genus *Actinometra*, Müll., with a morphological account of a new Species (*A. polymorpha*) from the Philippine Islands.

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(Abstract *.)

The name *Actinometra* was given by Johannes Müller† to those species of the genus *Comatula* (Lamarck) in which the tentacular furrows of the arms unite on the disk into less than five principal trunks or ambulacra converging towards the peristom. Until the time of Müller, Leach's genus *Alecto* was used as equivalent to the *Comatula* of Lamarck; but the application of this name was limited by Müller, who used it in contradistinction to *Actinometra*, to describe the more common species of *Comatula*, in which five principal groove-trunks or ambulacra radiate outwards from the peristom, and subdivide symmetrically into more or fewer branches proceeding to the different groups of arms.

The position of the mouth in *Alecto* might be either subcentral (in no *Comatula* is it absolutely central), or more or less excentric, sometimes even marginal; but any *Comatula* in which five ambulacra reached the peristom, whatever the position of the mouth, was referred by Müller to this genus, the sole distinction between it and *Actinometra* being the presence of five or fewer principal ambulacral trunks.

From the time of Müller until now, the genus *Actinometra* has remained as he left it, though more than one author has remarked upon the unsatisfactory nature of its distinctive characters. Leach's name *Alecto*, however, has gradually passed into disuse, having been partially replaced by De Freminville's name *Antedon*, a precise definition of which has been given by Mr. Norman‡.

Antedon, like *Alecto*, was originally equivalent to *Comatula*; but, according to Mr. Norman's definition (which has been universally adopted), it is now used to designate those forms only in which

* [The memoir in full, with illustrations, will subsequently appear in the Society's Transactions.—Ed.]

† "Ueber die Gattung *Comatula*, Lam., und ihre Arten," Abhandlungen der Berlin. Akademie, 1849.

‡ "On the Genera and Species of the British Echinodermata," Ann. & Mag. Nat. Hist. ser. 3, vol. xv. p. 98.

the mouth is subcentral. All these, as for example the British *Antedon rosacea*, have the five centripetal ambulacra characteristic of *Alecto*; but there are many species of *Alecto*, as for example *C.* (*Alecto*) *multiradiata*, in which the five primary ambulacra converge to an excentric or even marginal peristomial area, the mouth being nowhere near the centre of the disk. Such forms as these clearly have no place in the genus *Antedon*, while they are excluded from *Actinometra*, as defined by Müller, although agreeing with it in the excentric position of the mouth. In many *Comatulæ* also, the mouth is excentric, and six, eight, or even ten groove-trunks reach the peristom; these, again, have no place either in *Antedon*, *Alecto*, or *Actinometra* (as defined by Müller).

After a careful examination of a large number of *Comatulæ*, including the valuable collection in the Paris Museum, and also a number of new species brought by Professor Semper from the Philippine Islands, the author has been led to the conclusion that Müller's mode of classification of the *Comatulæ* is purely artificial, and leads to the separation of individuals which really belong to one and the same species: on the other hand, the position of the mouth, either subcentral or excentric, affords a very natural means of classification, being readily visible externally, and being also accompanied by important differences in the anatomy and relative positions of the internal organs.

The author has examined eleven specimens of *Comatula polymorpha*, in all of which the mouth is excentric, and the composition of their skeleton and other parts so similar that they evidently belong to one species. One of them, however, would have been referred to *Alecto* by Müller, having five primary groove-trunks, and another, with only four, to *Actinometra*; but there is no place in his system for the remainder, which have six, seven, or eight groove-trunks reaching the excentric peristom. Müller himself affords us similar examples of the artificial nature of his classification; for in one place he describes a specimen as *Actinometra*, while a little further on he classes it as *Alecto*, on account of the similarities it presents to *A. multiradiata* in the characters of the skeleton.

Again, Müller, who examined the Paris collection of *Comatulæ*, does not describe the *C. trichoptera* which he found there, either as *Alecto* or as *Actinometra*, the reason probably being that there are only four primary groove-trunks in one of the two specimens,

while in the other there are five, the mouth being excentric in both cases.

These and many similar instances have led the author to the conclusion that the real distinction between *Antedon* and *Actinometra* lies in the subcentral or excentric position of the mouth, and that the number of groove-trunks reaching the peristom is a character of very minor importance. The definition of *Actinometra*, therefore, will have to be extended so as to include those forms in which there are five or more primary groove-trunks, as well as those forms with less than five, for which the name was originally introduced by Müller.

After arriving at the above conclusion, the author learnt from Dr. Lütken, of Copenhagen, that he had held similar views for some time past. Dr. Lütken further informed the author that *Antedon* and *Actinometra* also differ from one another in the character of their oral pinnules. In the former genus, with the mouth subcentral, the oral pinnules are but slightly differentiated from those of the rest of the arm, while in *Actinometra* they are always very different from the others, being more or less flagelliform with small lateral shield-shaped processes on their terminal joints, which thus have a comb-like appearance.

Although, like Dr. Lütken, the author has found that in all the *Comatulæ* he has examined the terminal comb on the oral pinnules invariably coexists with an excentric mouth, and is absent in those forms with a subcentral mouth, yet this does not seem always to be the case; for Lovén* has described a new *Comatula* under the name of *Phanogenia*, in which the mouth is central, but the oral pinnules have a terminal comb.

This form is perhaps generically distinct from *Antedon* and *Actinometra*, as it presents some peculiarities in the structure of the skeleton; but in a new American species described by Pourtales† this is not the case, and the mouth is excentric, while the oral pinnules are not specially distinguished: the same appears to be the case in the *Comatula rosea* of Müller; and the author is therefore not disposed to attach very much importance to the presence or absence of a terminal comb on the oral pinnules as a

* Phanogenia, ett hittills okändt slägte af fria Crinoideer. Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar, 1866, No. 9, pp. 223–233.

† "List of the Crinoids obtained on the coasts of Florida and Cuba, by the United-States Coast-Survey Gulf-Stream Expeditions, in 1867, 1868, 1869" ('Bulletins of the Museum of Comparative Zoology,' Cambridge, U.S., No. 11).

distinctive character between *Antedon* and *Actinometra*. The differences in the position of the mouth, however, afford a distinctive character of much value, especially as they are accompanied by marked variations in the anatomy and mutual relations of important internal organs.

Out of the numerous species of *Comatula* at present known, the author has been able to refer seventeen to the genus *Actinometra* as above defined. Fourteen of these were known to Müller; and out of the remaining twenty-three species described by him, the author has determined sixteen as true *Antedons* with a subcentral mouth, together with nine species described by various authors since the publication of Müller's memoir. Seven of Müller's species remain as yet undetermined, together with one described by Pourtales, as there is no mention of the position of the mouth in the specific diagnoses, and the author has been unable to make a personal examination of the specimens in question.

Taking, therefore, the genus *Actinometra* as including all those *Comatulæ* in which the mouth is excentric, the author finds that it may be divided into two principal groups according to the position of the mouth with respect to the radial or ambulacral planes. In *Antedon*, where the mouth is subcentral, the interradial area containing the anal tube may be considered as posterior; and a plane passing through the mouth and anus so as to divide the disk into two symmetrical halves, will traverse the odd ambulacrum in front of the mouth, which may therefore be regarded as radial in position.

In *Actinometra solaris* the odd ambulacrum is also in front of the mouth, which, though excentric in position, lies in the radial half of a plane passing through the mouth and anus, so as to divide the disk into two symmetrical halves, the interradial half of this plane passing through the anus.

In *Act. multiradiata*, however, and in many other species, the case is different, as the mouth is interradial in position, and the odd ambulacrum lies behind it; for a plane cutting the mouth and anus is radial behind the mouth, in front of which it passes along the interval between two ambulacra or radii.

This type of *Actinometra*, in which the mouth is interradial and the odd ambulacrum lies behind it, is considerably more frequent, so far as the author's experience goes, than the simpler type, in which the mouth is radial and the odd ambulacrum anterior, as in

Antedon: he has only met with this last in *A. solaris* and its varieties, in *A. fimbriata*, and in three new species of *Actinometra* from the West Indies; all the other species known to him belong, like *A. multiradiata* and *A. polymorpha*, to the type in which the mouth is interradial and the odd ambulacrum posterior.

The median line of the ventral perisom of all the arms of *Antedon* is occupied by an open ambulacral groove bounded by an elevated fold of perisom, the edge of which is not straight, but cut out into a series of minute valvules, the crescentic or respiratory leaves. At the base of each leaf, and to some extent protected by it, is a group of three tentacles, one of which, the more distal, is larger than the other two. This trifid group of tentacles and the cavity of the respiratory leaf in connexion with them, are in communication with the cavity of the radial water-vessel by a common lateral branch: the tentacular groups alternate on the opposite sides of the ambulacral groove, from the base to the tip of each arm, and are distributed in the same manner at the sides of the ambulacra of the disk. The floor of each groove consists of a layer of ciliated epithelium, beneath which lie the radial water-vascular and blood-vascular trunks, but separated from it by a fibrillar structure (the subepithelial band), to which a nervous character has been attributed by the author and by all the other observers who have described it.

In *Act. polymorpha* and in many other *Actinometræ* the above description only applies to the more anterior arms; for the arms of the posterior radii are usually entirely devoid of tentacles, and in many of them the ventral perisom not only exhibits no ambulacral groove, but is convex as in the oral pinnules of *Antedon*.

In neither of the two large aboral groove-trunks which form a horseshoe-shaped curve enclosing the anal area of *Act. polymorpha*, are the tentacular groups so well developed as in the two anterior ambulacra. The bases of these trunks, where they start from the peristom, are of the usual character; but sooner or later the tentacles become more and more insignificant, and finally disappear altogether, while the position of the crescentic leaves is only indicated by a very faint wavy line at the edge of each groove. In small specimens with but few arms, the grooves of the posterior and posterolateral arms may remain in this condition; but in larger specimens with many arms all trace of the respiratory leaves disappears, and the two edges of the groove gradually approach one another and finally unite, so that the ventral surface of the

arm and pinnules becomes convex, and does not show the least trace of a groove of any description.

The position of the point at which the two folds of perisom bounding the original ambulacral groove meet and unite, varies extremely: the union may, though rarely, take place on the disk; sometimes it is at the base of the arms, and sometimes not till near their middle or terminal portions. In any case, however, the fusion where it occurs is so complete that *all trace of the original ambulacral groove is entirely obliterated.*

This fact has a very important bearing upon the two opposite views which have been recently advanced regarding the nervous system of *Comatula.*

According to the one view, held by Dr. Carpenter and by the author, the axial cords traversing the centre of the calcareous segments of the skeleton, together with the fibrillar envelope of the quinquelocular organ from which they all radiate, constitute the principal and, as the author is disposed to think, the *only* nervous system of *Comatula.*

In the centre of every segment of the skeleton, from the first radials to the tips of the arms and pinnules, and also in the cirrus-segments, these axial cords increase considerably in size and give off four main branches. Two run towards the ventral side and in the calyx disappear in the neighbourhood of the muscles connecting the segments; but in the arms they continue their course towards the ventral perisom and break up into numerous small branches, some of which may be traced as far as the tips of the crescentic leaves. The two inferior or dorsal trunks run towards the dorsal surface of the skeleton; and while some of their branches are lost in the plexus of tissue forming its organic basis, others seem to become connected with epidermic structures. In the arms of *Antedon celtica* Dr. Carpenter has found branches of the axial cords ramifying upon the ends of the muscular bundles connecting the segments; and the results of his experiments have shown that the power of motion in any arm depends upon the connexion between its axial cord and the fibrillar envelope of the chambered organ, while the power of coordinating the regular swimming movements of all the arms depends upon the integrity of this envelope, which there is thus good reason to believe to be of a nervous nature.

The chief objection to this view is that it places the nervous system of the Crinoids on the dorsal side of the body, and not on the ventral side immediately superior to the water-vessel as in

all the other Echinoderms. This objection has been strongly urged by various German authors, who all assign a nervous character to the fibrillar subepithelial band above mentioned, since it occupies the same relative position as a very similar structure that has been hitherto generally regarded as representing the nervous system of the Asterids. It extends along the ventral surface of the arms and pinnules beneath the ambulacral grooves, and forms a ring round the mouth beneath the ciliated epithelium of the peristomial area, just above the water-vascular and blood-vascular rings. This band was discovered independently and nearly simultaneously by the author and by three German observers, all of whom regard it as representing *the* nervous system of *Comatula*, and deny the nervous nature of the axial cords. Dr. Carpenter's experiments at Naples*, however, have fully proved that the coordinated swimming-movements of the arms are entirely independent of this subepithelial band, and are carried on even when the visceral mass containing the oral ring is entirely removed from the calyx; so that this structure, if a nerve at all, cannot be regarded as motor in function. It gives off no branches, except an extremely minute one beneath the epithelium of each respiratory leaf and tentacular group.

If, however, the axial cords are not nerves, and if these ventral subepithelial bands are to be regarded as the only nervous structures in the whole Crinoid organization, the difficulty presents itself that the oral pinnules of the European Crinoids, and more than half the arms, with the majority of the pinnules of some forms of *Actinometra*, are entirely devoid of a nervous supply.

The oral pinnules of *Antedon* have been shown by Dr. Carpenter to be extremely susceptible of irritation. When they are touched in the living animal, the whole circlet of arms is suddenly and simultaneously coiled up over the disk, while irritation of one of the ordinary pinnules is simply followed by flexion of the arm which bears it.

The structure of these oral pinnules, which are borne in *Antedon rosacea* by the second brachials, differs very considerably from that of the pinnules borne by the other brachial segments; for not only are they sterile, but they have neither tentacular apparatus nor ambulacral groove, their ventral surface being slightly convex, while the ordinary ciliated epithelium of the groove with the subjacent subepithelial band, the so-called "ambulacral nerve," are

* Supplemental Note to a paper "On the Structure, Physiology, and Development of *Antedon rosaceus*," Proceedings R. S., No. 169, 1876.

entirely absent. This condition, which is limited in *A. rosacea* to the oral pinnules, sometimes exists in whole arms, and in all the pinnules borne by them in some species of *Actinometra*: even in the arms which come off from the anterior or oral side of the disk, the ambulacral groove does not give off regular branches to the pinnules borne by the third and successive brachial segments; but a variable number of these first pinnules, sometimes only three or four, sometimes as many as forty, resemble the oral pinnules in this respect, their ventral surface being convex and devoid of any ciliated epithelium or subepithelial band, while their water-vessel is simple without any lateral extensions to respiratory leaves and tentacles. In these oral arms, however, branches of the ambulacral grooves enter the pinnules sooner or later, so that the terminal ones are always provided with a distinct tentacular apparatus, while the floor of their median groove is of the usual character, consisting of a ciliated epithelium and a subepithelial fibrillar band. We have already seen that in many cases the ambulacral grooves going to the aboral arms become less and less distinct as they get further and further from the peristom, and that their tentacles diminish and finally disappear: at the same time the floor of the groove becomes very much reduced, its epithelial layer thinner and thinner, and the subepithelial band almost invisible, until, in those cases in which the sides of the groove meet and unite, the ciliated epithelium and subepithelial band or ambulacral nerve disappear altogether, as in the oral pinnules. Consequently, when this union takes place on the disk, *whole arms must be entirely devoid of any nervous supply*, unless we admit the nervous nature of the antiambulacral axial cords.

In such cases it would naturally be expected that these posterior arms would not perform the regular swimming-movements, like those anterior arms which have an open tentacular groove and a subjacent "ambulacral nerve;" but Professor Semper, who has kept *Actinometræ* in his aquaria for weeks together, has informed the anthor that he never saw the least trace of any irregularity in the alternating movements of their arms when swimming.

If we suppose, with Ludwig*, that the subepithelial band is the sole structure of a nervous nature in the whole Crinoid organization, it is difficult to understand the fact (which Ludwig himself

* 'Morphologische Studien an Echinodermen. I. Beiträge zur Anatomie der Crinoideen,' Leipzig, 1877, p. 81 (Separat-Abdruck aus der Zeitschrift für wissenschaftliche Zoologie, Bd. xxviii.).

admits) that it gives off no branches except the very small ones which go to the tentacles. It is true that in the *Ophiuridæ* the radial ventrally-placed nerve does give off branches which go to the muscles, besides those proceeding to the tentacles, as described by Lange*, Teuscher†, and Simroth‡; but the researches of the first-mentioned observer render it very doubtful whether the representative in the *Ophiuridæ* of the subepithelial band of *Comatula* takes any part in the formation of these branches.

That the subepithelial band is of the same nature in the Crinoids and Asterids there can, it seems, be little doubt; and it is therefore somewhat interesting that its nervous nature in the Asterids has recently been disputed by Lange §, who regards as nervous only two cellular masses separated from the subepithelial fibrillar band by a connective-tissue membrane, and projecting into the lumen of the nerve-canal, which swell under the pigment-spot into a large ganglionic mass; while the subepithelial band, together with the ciliated epithelium and the cuticula, constitutes a protecting integumentary layer.

Lange finds a corresponding condition in *Ophiura texturata*, in which the radial nervous system is better developed than in the Asterids, and consists of a series of paired ganglionic masses connected with one another by transverse and longitudinal commissures. On the ventral side of this ganglionated cord is a longitudinal band, which Lange regards as the homologue of the protecting integumentary layer forming the floor of the ambulacral groove of the Asterids, and which, as universally admitted, corresponds to the subepithelial band, epithelium, and cuticula of the ambulacral grooves of the Crinoids.

Lange's views have been partially accepted by Simroth ||; but they have been altogether denied by Teuscher¶, who regards Lange's nervous cell-masses in the Asterids simply as an epithelial layer several cells deep on the inner wall of the nerve-canal, while the terminal ganglionic mass under the eye-spot is represented by Teuscher as a cushion of connective tissue.

* "Beiträge zur Anatomie und Histiologie der Asterien und Ophiuren," Morphologisches Jahrbuch, Band ii. 1876, p. 241.

† "Beiträge zur Anatomie der Echinodermen.—II. Ophiuridæ," Jenaische Zeitschrift, Band x. 1876, p. 274.

‡ "Anatomie und Schizogonie der *Ophiactis virens*, Sars," Theil I., Zeitschrift für wissenschaftliche Zoologie, Band xxvii. p. 473.

§ *Loc. cit.* p. 274. || *Loc. cit.* pp. 556, 560.

¶ 'Beiträge,' &c. III. "Asteriden," Jen. Zeitschr. x. p. 513.

Still less do Teuscher and Lange agree about the nervous system of the Ophiurids. Lange's ganglionic masses are described as artificial by Teuscher, who, as in the case of the Asterids, regards as the nerve only the fibrillar structure representing the subepithelial band of *Comatula*.

The question is still an open one: and it is therefore of no small interest to find that this subepithelial band, the so called ambulacral nerve, is not always present in the arms of *Comatula*, and that even when it exists it is certainly not motor in function.

It has been stated above that in certain of the arms of *Actinometra* the water-vessels are simple tubes like the integumentary water-vessels of the Molpadidæ, and not in connexion with any tentacular apparatus. Whether the mouth be radial or interradial, the non-tentaculiferous arms are the aboral ones; so that in the latter case they belong to the trivium, as in *A. polymorpha*, and in the former to the bivium, as in *A. solaris*.

In only one out of twelve specimens of *A. polymorpha* has the author found a non-tentaculiferous arm in the bivium: it was in one of the two anterior radii. But this specimen was very remarkable; for out of 31 arms 19 were entirely devoid of a tentacular apparatus, and in 15 of these the union of the two sides of the ambulacral grooves had taken place either on the disk or in the basal arm-segments; so that an "ambulacral nerve" was wanting in nearly half the total number of arms. In the other four of these non-tentaculiferous arms the groove remained open for a short distance, and then closed in the manner already described. Three of these four arms belonged to the trivium; but the fourth was an anterior arm belonging to the bivium, and was borne upon the same palmar axillary as a well-developed ordinary tentaculiferous arm.

With this exception, the author has invariably found the non-tentaculiferous arms on the aboral side of the disk: their number and distribution, however, vary extremely, not only in different species, but in different individuals of the same species. Thus in *A. polymorpha* the author has found the proportion of non-tentaculiferous arms to the total number to vary from $\frac{6}{20}$ to $\frac{19}{31}$. Even in two individuals with the same number of arms it may not be the same: thus in two specimens with 20 arms the proportion was $\frac{6}{20}$ and $\frac{11}{20}$ respectively, and again $\frac{10}{28}$ and $\frac{15}{28}$; while in one specimen all the arms were normal and tentaculiferous as in *Antedon*.

The same variation occurs in *Actinometra solaris*, in which species the number of arms is limited to 10: they may be all tentaculiferous; or from one to four of the posterior arms may have no tentacular apparatus. This abnormal condition does not seem, however, to be very common; for out of all the *Actinometræ* in the Paris collection the author found but one in which he could say with any certainty, without cutting sections, that some of the posterior arms were non-tentaculiferous; and this was a large many-armed specimen of *A. Bennetti*, Müller.

The condition of the ambulacral groove and of the tentacular apparatus is not the only point in which the anterior or oral arms of *Actinometra* may differ from the posterior or aboral arms. The former taper very slowly, contain far more segments, and are much longer than the latter, while the form of their terminal portions, and of the pinnules which these bear, is altogether different.

In *A. polymorpha* the centre of the dorsal half of each of the segments of the terminal pinnules of the posterior arms is often occupied by a dark brown ovoid body of a peculiar cellular nature, which the author has reasons for believing to be a sense-organ. These bodies may also, though rarely, occur in one or more of the anterior tentaculiferous arms; but they do not exist in all the specimens of *A. polymorpha* which the author has examined, for in 7 out of 12 specimens they are entirely wanting.

The arms of *A. polymorpha* may therefore be roughly classified as follows:—

1. *Anterior.*—120–150 segments: pinnules increasing in length to the terminal ones, which are very long and slender. Tentaculiferous.

2. *Anterolateral.*—Also tentaculiferous: 100–120 segments: terminal pinnules long and slender.

3. *Posterolateral.*—80–100 segments: terminal pinnules stout, but rather longer than the median ones. Ventral perisom with narrow ambulacral grooves, but non-tentaculiferous.

Posterior.—Only 60–80 segments: terminal pinnules stout, but decreasing slightly in length from the middle of the arm onwards. No ambulacral grooves nor tentaculiferous apparatus.

Another difference between the anterior and posterior arms is that the genital glands of the latter are far more developed than in the former. Not only is their number greater, although the total number of pinnules on a posterior arm may not be much

more than half that on an anterior arm, but they also attain a very much greater size, the basal and median pinnules of an anterior arm being very much less swollen than the corresponding pinnules of a posterior arm. A similar inequality in the development of the genital glands has been noted by Agassiz as occurring in the Echini *.

The external appearance of the centrodorsal piece of *Actinometra* is very characteristic: like the cirri which it bears, it is far more constant throughout a considerable range of species from very various localities than it appears to be in the individual members of a single species both of the European and of some of the foreign *Antedons* even when collected in the same locality.

In *Actinometra* the centrodorsal piece is almost invariably a flattened, circular or rudely pentagonal disk, somewhat hollowed in the centre, and with low sloping sides marked out into distinct sockets for the articulation of the cirri, which are limited to its margin, the central portion of the plate being entirely free from them. There is usually only one row of cirrus-sockets at the margin of the plate; but in the large *A. robusta* there may be two, and even traces of a third. In the typical forms of *A. polymorpha* the number of cirri existing at any one time seems to vary between 15 and 25; and the size and number of their segments are tolerably constant, which is by no means the case in *Antedon*. Further, the individual segments do not acquire the characters of maturity at any thing like such an early date as they usually do in *Antedon*, but even after the cirrus has attained a considerable size and has the normal number of segments the latter remain of a very rudimentary character, which is a somewhat exceptional mode of development in *Antedon*.

Another very marked difference between *Antedon* and *Actinometra* consists in the fact that in the latter genus the planes of the external or distal faces of the first radials are parallel to the vertical axis of the calyx, and not inclined to it at a considerable angle as is the case in *Antedon*; so that the whole of the ventral surface of the calyx is in one horizontal plane, while in *Antedon* the second and third radials and the bases of the arms are at a much higher level than the pentagon of the first radials, owing to the inclination of the distal articular faces of the latter.

The most interesting point in the skeleton of *Actinometra* is the condition of the rosette or metamorphosed basals, which re-

* 'Revision of the Echini,' pt. iv. pp. 680, 681.

tain far more of an embryonic character than is usually the case in *Antedon*; but the author has met with specimens of *Ant. rosacea* in which the metamorphosis is far less complete than usual, and which present in this respect an approximation to *Actinometra*. A normal rosette of *Antedon rosacea* consists of a disk perforated in the centre, with ten rays proceeding from it. Five of these rays are short, triangular in form, and nearly flat; and their position is interradial, as they are directed to the sutures between the five radials, their apices joining the contiguous pairs of these just between the two adjacent apertures of the central canals. Alternating with these five interradial processes of the rosette are five radial spout-like processes, each of which has parallel margins inflected on its ventral aspect in such a manner as to form a groove, while the process itself is so curved towards its dorsal aspect that this groove reaches the periphery of the rosette and then terminates abruptly as if truncated.

The inflected margins of each of these five radial processes of the rosette are applied to the similarly inflected margins of the dorsal half of an axial furrow lying between the two apertures of the central canal on the internal face of each first radial, so that the two grooves are united into a complete canal. Each of the five canals thus formed contains a diverticulum of the body-cavity; and they terminate blindly in shallow depressions upon the ventral surface of the centrodorsal piece on which the first radials rest.

The rosette is essentially formed out of a secondary calcareous reticulation formed upon the ventral surface of the original basals. The primary or dorsal layer originally constituting them becomes almost entirely absorbed, the ends of the spout-like processes being all that remains of them in the adult *Comatula*; for the salient angle of each basal plate which is received between two first radials and the greater part of the centre of its dorsal surface is usually entirely removed.

Sometimes, however, the removal of the primary or dorsal layer at the salient angle of one or more of the five embryonic basals may be incomplete, so that the ends of the curved rays of the rosette exhibit lateral processes which are the remains of the upper margins of the primitive basal plates on which the first radials rested. Occasionally the apex of the original basal is left unabsorbed, so that the two lateral curved processes which persist after the removal of the primary external layer along the

median line of each plate remain in connexion with one another. Not unfrequently the triangular interradial process, which is developed from a secondary calcareous deposit on the ventral side of the original basal, becomes more or less completely united with these primary bars connecting the lateral portions of the basal. The latter retain their primitive relation to the first radials; for they remain united with them along the inner margins of their dorsal surfaces; and as they partially cover in the dorsal aspect of the bifurcating nerve-cords which enter the central canals of the first radials, the author has called them the basal bridge. The interradial processes of the rosette of *A. rosacea* may also exhibit departures from their normal triangular shape: not unfrequently they become long and spout-like, with inflected parallel margins, which are so applied to the projecting and similarly inflected outer edges of the adjacent openings of the central canals in two contiguous radials as to convert the interradial furrow lying between them into a complete axial interradial canal, precisely similar in character to the axial radial canals already described.

This occasional spout-like condition of the interradial processes of the rosette of *A. rosacea* is of considerable interest, as it is normal in *Actinometra*, in which genus also the ends of the alternating radial and interradial processes are always connected by a basal bridge, the unabsorbed remains of the outer margins of the embryonic basal plate.

From the outer ends of each of the interradial processes of the rosette of *Actinometra*, where it unites with the two bars of the basal bridge proceeding from the radial process on either side, there extends, for a longer or shorter distance towards the periphery of the calyx, a prismatic or cylindrical rod, which is received in an interradial furrow on the ventral surface of the centrodorsal piece. These five rods, to which, taken together, the author has given the name of the basal star, vary very greatly in the degree of their development, not only in different species, but in different individuals of the same species, and to some extent also in the same individual.

The reason of this is that these rods are not like the other pieces of the skeleton, calcifications in a nucleated protoplasmic network, but they are simply formed by a more or less complete deposition of calcareous matter in the five interradial planes around the fibres of connective tissue which effect the synostosis of the

centrodorsal piece with the pentagonal base of the calyx. In one specimen of *A. polymorpha* the author has found them to be almost entirely absent, while in others they are very large and stout. Lovén has found something of the same kind in *Antedon Eschrichtii*; but in both the specimens of this species which the author has been able to examine, they were scarcely developed at all.

These tertiary elements in the basals of *Actinometra* are of extreme interest; for they are precisely similar in shape and position to the basals of two species of the fossil genus *Solanocrinus*, viz. *S. costatus* and *S. scrobiculatus*.

In both these species there seems to be no rosette; but the basals consist of five prismatic rods in contact by their central ends, and occupying five deep grooves on the ventral surface of the centrodorsal piece. They extend beyond its margin, however, and so become visible on the exterior of the calyx, which is not the case with the rays of the basal star of *Actinometra*. Hence this would seem to preclude the possibility of their being formed like the latter, by ossification in the connective tissue of the synostosis between the radial pentagon and the subjacent centrodorsal piece; so that they are probably the remains of the original embryonic basal plates, which are represented in *Actinometra* only by the rosette: and the rays of the basal star of *Actinometra* would therefore not be strictly homologous with the rod-like basals of *Solanocrinus costatus*, although the analogy in their position is complete.

The calyx of *S. Jaegeri* presents a great advance upon that of *S. costatus* with respect to the development of the basals, which led Pictet* to propose the erection of this species into a separate genus. Instead of being long and narrow, and in contact only by their central ends, as in *S. costatus*, they are broad and wedge-shaped, and in contact along their whole sides, so as to form a complete calcareous disk entirely separating the radial pentagon from the centrodorsal piece.

This is precisely their position in *Pentacrinus*, though there are but few species of that genus in which the basals are relatively so large and complete as in *S. Jaegeri*. In *P. asteria* and in the two fossil species *P. briareus* and *P. subangularis* they are small and cuneiform, and only in contact by their central ends, just as in *S. costatus*; so that the greater portion of the radial pentagon is

* 'Traité de Paléontologie,' tom. iv. p. 288.

in contact with the top stem-segment: in *P. Mülleri* they are in contact for about half their length and then diverge, while in *P. Wyville-Thomsoni* they are completely united with one another along the whole length of their sides, so as entirely to cut off the radial pentagon from the top stem-segment, just as in *S. Jaegeri*. There can therefore be little doubt that the basals of *Pentacrinus* are homologous with those of *Solanocrinus*, and therefore analogous, as a whole, to the compound basals of *Actinometra*, which are not entirely developed out of the embryonic basal plates. Only their central part, the rosette, has the same origin as the basals of *Pentacrinus*, with the inner or central ends of which it is strictly homologous; for the bifurcating nerve-cords proceeding from the angles of the chambered organ have the same relation to the rosette and basal bridge of *Actinometra* as to the united central ends of the basals of *Pentacrinus*, which are perforated by bifurcating canals in which these cords are lodged.

It would seem, in fact, as if in *Pentacrinus* and *Solanocrinus* the embryonic basal plates became directly transformed into the basals of the adult; while in *Comatula* they undergo metamorphosis into the central rosette by the absorption of the greater portion of their dorsal or *primary* tissue, and the development of a *secondary* ossification on the ventral side of the original plates.

In *Antedon rosacea* the metamorphosis is much more complete than in *A. Eschrichtii* and in *Actinometra*, in which last new skeletal elements are developed by a more or less complete *tertiary* ossification in masses of connective tissue, that correspond precisely in position and also, to a certain extent, in shape with the basals of *Solanocrinus* and *Pentacrinus*. These, being most probably direct products of the growth of the embryonic basals, are therefore strictly homologous only to the rosette of *Actinometra*, although analogous in position to the whole circlet of compound basals in this genus, namely to the rosette and basal star taken together.

The recent genus *Comaster*, or *Comatula multiradiata* of Goldfuss*, from the Indian Ocean, has been considered by most authors generically identical with the fossil *Solanocrinus*, on account of the appearance of the basals upon the exterior of the calyx.

The condition of the central ends of the basals, however, and, in fact, of the whole calyx, is very remarkable and very unlike that presented by any other *Comatula* with which we are acquainted,

* Petrefacta Germaniæ, i. p. 202.

while the differences between it and *Solanocrinus* are so very great that it is difficult to understand how they can ever have been regarded as belonging to one and the same genus.

The centrodorsal piece of *Comaster* is hemispherical: but its margin is not infolded as a broad lip, forming a wide superior ventral surface on which the first radials rest. These last bear the axillaries directly without the intervention of any second radials, which are always present in *Comatula*, and have very narrow inferior faces that simply rest upon the thick rim of the hemispherical centrodorsal basin. The infero-lateral angles of every pair of contiguous radials are truncated; and the spaces left between them when they are in their natural condition of apposition by their lateral faces, are occupied by the five small triangular basals which rest on the rim of the centrodorsal basin, and are visible on the exterior of the calyx alternating with the first radials, just like the peripheral ends of the basals of *Solanocrinus costatus*. In this species, however, the basals are longish rods of considerable relative width and in contact by their central ends, while in *Comaster* they are small triangular pieces, from the middle of the inner and lower edge of each of which there arises a tooth-like process in the shape of a small cartilaginous rod extending to the centre of the centrodorsal piece which is grooved to receive it.

Goldfuss does not describe any thing that could be regarded as a rosette in *Comaster*; and the small triangular basals would seem to be the ultimate condition of the embryonic basal plates, with which they exactly agree in their relative position; but the relations of their central processes are somewhat difficult to understand. They can hardly be regarded as comparable, except in their interradial position, to the rays of the basal star of *Actinometra*; for they lie in grooves on the floor of the cavity of the centrodorsal basin, and are apparently independent of the first radials, which have no extensive area of synostosis with the centrodorsal piece as in *Comatula*—while from Goldfuss's account of them they do not seem to be calcified, but to be more of a cartilaginous nature.

It is possible that the calyx of *Antedon Dübenii*, as described by Böhlsche*, may present some points of resemblance to that of *Comaster*; for, as in this genus, only two rows of radials are visible externally, and between every two radials of the first row is a

* "Ueber *Actinometra Bennettii* und eine neue Comatula-Art (*Antedon Dubenii*)," Wiegmann's Archiv für Naturgeschichte, 1866, p. 94.

small calcareous ossicle. Böhlsche did not separate the pieces of the calyx, and was therefore unable to determine whether there are really three rows of radials, as in the ordinary *Comatulæ*, or not: but if, as in *Comaster*, there are only two rows, then the small ossicles appearing externally between every two pieces of the first row would represent the basals of *Comaster*. The condition of their central ends is unfortunately still unknown to us.

Comaster further differs from all the *Comatulæ* with which we are acquainted, and also from *Solanocrinus*, in the fact that the nervous cords are not lodged in canals which perforate the pieces of the calyx, but lie freely on the superior surfaces of the segments, the opposed terminal faces of which lie flatly against one another. The muscles and ligaments lie along their concave inner sides and cover in the freely exposed nerve-cords: from the palmar axillaries onwards, however, all the segments have articular surfaces of the usual character, and are perforated by central canals in which the nerve-cords lie. This condition of the segments of the calyx of *Comaster* is of great interest; for, besides being the normal permanent condition in the tessellate Crinoids, it is the embryonic condition, so far as the position of the nerve-cords is concerned, in *Comatula*.

These facts will suffice to show the very great differences that exist, in the skeleton alone, between *Comaster* and the other members of the family Comatulidæ, including *Solanocrinus*—with which genus it has been united, on account of the appearance of the basals on the exterior of the calyx. In *Solanocrinus*, however, as in the other Comatulidæ, the first radials are perforated by central canals for the nerve-cords; and the absence of this character in *Comaster* would alone justify our referring these two forms to separate genera, even were this the only difference between them, which, as shown above, is by no means the case.

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[Read June 21, 1877.]

(Plate XXII.)

In the collection of Accipitres submitted to me by Dr. Meyer, and obtained by him during his voyage to Papuasia, there was a